

BETWEEN-HABITAT DIFFERENCES IN HERBIVORE IMPACT ON CARIBBEAN CORAL REEFS

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ABSTRACT

Transplanted sections of the seagrass Thalassia testudinum were used as a bioassay to assess between-habitat differences in herbivory on three Caribbean reefs. Consumption of Thalassia by herbivorous fishes on shallow (1-10 m) reef slopes was significantly higher than on deep (30-40 m) reef slopes or on shallow reef flats. Seaweeds typical of reef flat habitats were rapidly consumed when placed on shallow reef slopes. Seaweeds typical of either deep or shallow reef slopes were relatively resistant to herbivory and a high proportion of these species are known to contain secondary chemical compounds that appear to deter herbivorous fishes. Shallow reef flats provide seaweeds with a predictable spatial escape from major reef herbivores; algae characteristic of these habitats have evolved few, if any, characteristics that significantly reduce losses to herbivory.

INTRODUCTION

Although herbivory plays a major role in determining the distribution and abundance of seaweeds on coral reefs (Stephenson and Searles 1960; Randall 1961, 1965; Ogden et al. 1973; Hay 1981a, b; Luchenco and Gaines 1981; Hay et al. 1983), few studies have addressed spatial variations in herbivory or the relative susceptibility to herbivory of seaweeds from different habitats. Recent investigations have focused on between- and within-habitat variations in herbivory on individual reefs (Hay 1981a, b; Hay et al. 1983) and on changes in herbivory that occur over depth gradients on several reefs scattered throughout the Caribbean (Hay 1984).

In this study we use transplanted sections of the seagrass Thalassia testudinum as a bioassay for herbivore activity in different habitats [reef flats, shallow (1-10 m) reef slopes, and deep (30-40 m) reef slopes] on 3 Caribbean reefs. We also transplant seaweeds from each of these habitats into areas with high herbivore activity in order to assess their relative susceptibility to herbivory.

METHODS

Thalassia was chosen as the bioassay organism because it is eaten in the field by both herbivorous fishes and urchins (Randall 1965, Ogden et al. 1973, Ogden 1976) and it is readily available on most reefs. Freshly collected sections of Thalassia were fastened in wooden clothespins; the latter were attached to small coral fragments and distributed haphazardly within the habitats where herbivory was to be measured. All Thalassia sections were 5 cm long and separated by a distance of 1-3 m when placed in the field. At the end of each

bioassay, removal of Thalassia was quantified by measuring the remaining length of each blade to the nearest .5 cm. During all tests, the clothespin and coral apparatus was positioned so that it would be equally approachable by both fishes and urchins. However, on most sections of these reefs, urchins are relatively uncommon and almost all Thalassia removal was due to grazing by fishes (Hay 1984).

Removal of Thalassia on reef slopes varies with depth; portions of this pattern have been extensively analyzed elsewhere (Hay et al. 1983, Hay 1984). In this paper we compare herbivory on (1) reef flats that are exposed at lowest tides, (2) shallow (1-10 m) portions of reef slopes, and (3) deeper (30-40 m) portions of reef slopes.

Seaweeds from each of these habitats were exposed to herbivorous reef fishes by placing small (3-4 cm long) pieces of each seaweed in a 3-stranded rope that was fastened to the reef slope at a depth of 1-5 m. Ten to 37 individuals of each test species were used at each location (for a description of each site, see Hay 1984). Seaweeds within a length of rope were separated from one another by a distance of about 7 cm. Thus, when an herbivore encountered a rope, all species of seaweed should have been equally apparent and available. At the end of an experiment, each species on each rope was recorded as either still present or totally eaten. Ropes were only placed in the field under completely calm conditions and were shaken to be sure that all individuals were securely attached. On the reef at Becerro, Honduras, where the feeding trial was of short duration (1.75 h), we were able to directly observe the ropes for most of the test period; no individuals were lost to any source other than herbivory. For the feeding trials of longer duration (19-24 h), we cannot absolutely rule out the possibility that some individuals were lost to breakage. However, the magnitude of such loss would have to be very small given the calm conditions and our inability to observe breakage during any of the observation periods.

Assignment of seaweeds as characteristic of reef flat, shallow reef slope, or deep reef slope habitats was based on qualitative observations at each study site. For example, species that were common between 30 and 40 m deep and present but rare at 10 m deep were listed as characteristic of the deep reef slope.

RESULTS

Consumption rates for sections of Thalassia placed on shallow reef slopes were significantly higher than consumption rates on either reef flats or deeper sections of reef slopes ($p < .05$, ANOVA and Student Newman-Keuls Test) (fig. 1). A deep reef slope comparison could not be done at Becerro, Honduras, since the reef slope extended to a depth of only 9 m. On all 3 reefs, all daytime removal of Thalassia was attributable to fishes, as evidenced by their crescent shaped feeding scars (see Hay et al. 1983, Hay 1984). On the two reefs where comparisons were made, removal of Thalassia on the deep reef slope was significantly higher than removal on the reef flat (fig. 1). However, the magnitude of this difference was small when compared to differences between the shallow reef slope and either of the other habitats.

When seaweeds were transplanted onto shallow reef slopes, those from reef flats were consumed rapidly while those from either deep or shallow reef slopes were consumed slowly if at all (fig. 2). The one exception to this pattern was Padina sp. at Becerro, Honduras (fig. 2C). This reef flat species was not eaten when placed on the shallow reef slope, although Padina sanctae-crucis was rapidly consumed at Carrie Bow and Lighthouse reefs (figs. 2A, 2B).

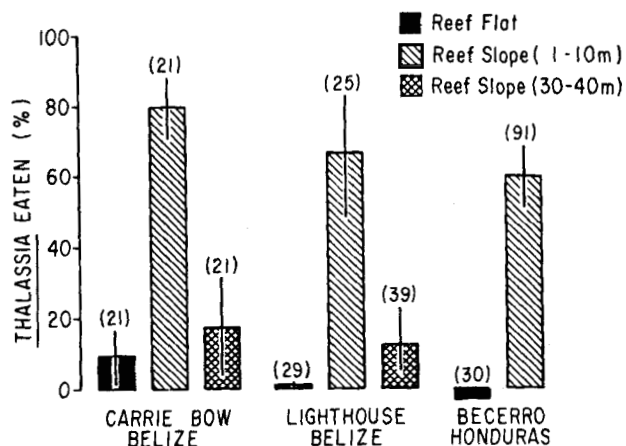
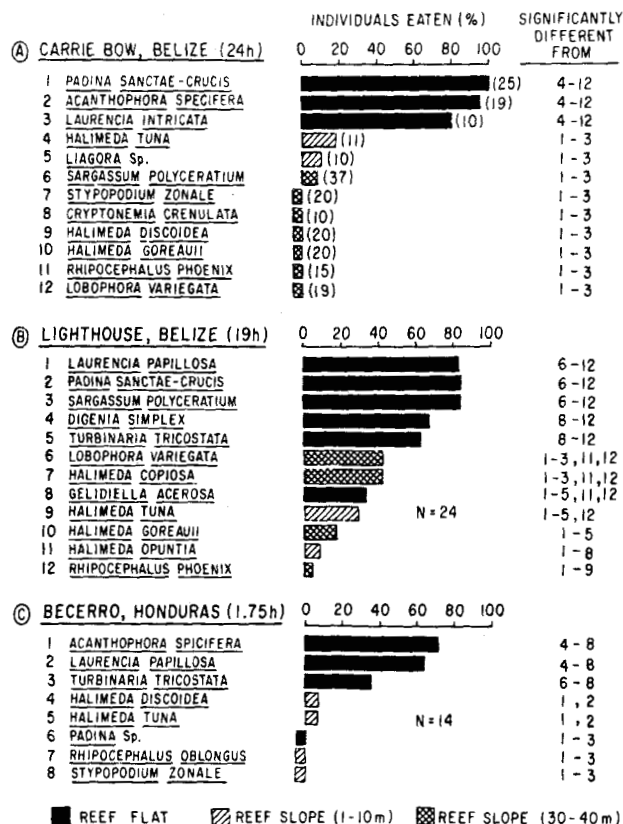


Fig. 1. The mean % of *Thalassia* eaten in different habitats on the 3 study reefs. Vertical lines represent ± 2 standard errors. Numbers in parentheses = N. At each reef, all differences are significant ($p < .05$, ANOVA and Newman-Keuls Test).

Susceptibility to herbivory of seaweeds from the shallow versus the deep reef slopes showed no consistent pattern. At Carrie Bow (fig. 2A), there were no significant differences between seaweeds from deep and shallow areas of the reef slope ($p < .05$, Fishers Exact Test). At Lighthouse (fig. 2B), there were some differences between species but these revealed no consistent between-habitat patterns.

For a given algal species, susceptibility to herbivory showed similar patterns on different reefs (fig. 2). There were, however, a few interesting exceptions. *Acanthophora specifera*, *Laurencia papillosa*, and *Padina sanctae-crucis* were consumed rapidly on each reef where they were tested. Species of *Halimeda* and *Rhipocephalus* were consistently resistant to herbivory, as was *Styopodium zonale*. *Turbinaria tricostrata* was of intermediate preference. *Sargassum polyceratum* from the reef flat on Lighthouse was very susceptible to herbivory (fig. 2B); *S. polyceratum* from the deep reef slope on Carrie Bow was very resistant (fig. 2A).



DISCUSSION

On the scale used in this study, between-habitat differences in herbivory are shown to be consistent on 3 different reefs (fig. 1). Rates of macrophyte removal on reef flats or on deep reef slopes are significantly reduced relative to removal rates on shallow reef slopes. In addition to the reefs studied here, shallow reef flats also have been shown to function as spatial escapes from herbivory in the Virgin Islands (Adey and Vassar 1975, Steneck and Adey 1976), the Netherlands Antilles (van den Hoek et al. 1978), and Panama (Hay 1981c, Hay et al. 1983). Decreased herbivory on deep reef slopes has been hypothesized to provide an explanation for the increased algal abundance that occurs at depth on some reefs (van den Hoek et al. 1978), and the rate of macrophyte removal recently has been shown to decrease with depth on a wide variety of undisturbed Caribbean reefs (Hay 1984).

Reef flats and deep reef slopes usually are characterized by reduced topographic complexity; in areas where predatory fishes are abundant, these more simplified habitats may be avoided by herbivorous fishes because they offer few places to hide when attacked by predators. On shallow reef slopes, herbivorous fishes concentrate their grazing in areas of greater topographic complexity (Hay et al. 1983) and, on heavily fished reefs where predatory fishes are relatively rare, herbivorous fishes make increased use of deeper reef slopes (Hay 1984). All of these patterns suggest that the probability of being preyed upon may play a significant role in determining the spatial pattern of foraging by herbivorous fishes.

Previous studies have suggested that the evolution of herbivore resistance in seaweeds involves costs that result in decreased growth rates and decreased competitive ability in the absence of herbivores (Lubchenco 1980; Lubchenco and Gaines 1981; Hay 1981a, c; Hay et al. 1983). The data presented in figure 2 provide a partial test of this hypothesis; if characteristics that promote herbivore resistance mandate costly tradeoffs, then herbivore resistance should not evolve in species that occur primarily in habitats subject to low rates of herbivory. Patterns exhibited by reef flat seaweeds support the hypothesis; they are subject to low rates of herbivory (fig. 1) and exhibit little resistance when exposure to herbivores is increased (fig. 2).

Rates of Thalassia removal on deep (30-40 m) reef slopes were significantly higher than on reef flats, but the magnitude of difference was not large--17.5% versus 9.3% at Carrie Bow, and 12.8% versus 1% on Ligvthhouse (fig. 1). However, differences in herbivore resistance of species from these habitats were striking (fig. 2). Despite the low rate of removal of Thalassia that was documented on deeper sections of the reef slope, seaweeds from these deeper areas were very resistant to herbivory. Even though the Thalassia bioassay shows herbivory to be relatively low in both reef-flat and deep reef-slope habitats, herbivore resistance appears to have been selected for on the deep reef slope and selected against on the shallow reef flat. This apparent paradox can be explained if one considers rate of biomass removal by herbivores (i.e., the Thalassia bioassay) relative to rate of production through photosynthesis. Seaweeds in shallow waters may grow many times faster than seaweeds in deeper waters (Hay 1981a, b). The low rate of biomass removal that occurs on reef flats can rapidly be replaced by photosynthesis since light is plentiful and turbulence prohibits the formation of large diffusion gradients that would slow nutrient acquisition (Doty 1971). Since production of seaweed biomass is very slow on deeper reef areas, even small losses to herbivores may exceed gains and thus select for increased herbivore resistance. As an example, if herbivores removed equivalent amounts of plant material from deep and shallow sites, selective

pressure for the evolution of grazer deterrents would be much greater in the deeper habitats since losses would be a larger proportion of net growth and take longer to replace. Future studies on spatial patterns in herbivory should attempt to quantify herbivore impact as a proportion of plant production within each habitat studied.

Most of the reef slope seaweeds are known to have naturally occurring chemical substances that appear to serve as defenses against herbivory (Fenical 1975, Norris and Fenical 1982). Many species in the genus Halimeda produce diterpenoid trialdehydes (Paul and Fenical 1983), Rhypocephalus contains similar compounds (Norris and Fenical 1982), Stypopodium zonale contains several related C₂₇ compounds derived from a mixed biosynthesis of diterpenoid and acetate precursors (Gerwick and Fenical 1981), and Liagora produces an unusual acetylene containing lipid (Norris and Fenical 1982). These compounds are toxic to or deter feeding in reef fishes, and some even stop cell division in fertilized sea urchin eggs or motility in sea urchin sperm (Norris and Fenical 1982, Paul and Fenical 1983). The polyphenolic compounds produced by Turpinaria and Sargassum (Norris and Fenical 1982) do not appear to be especially effective, as evidenced by the feeding data in figure 2. The difference in susceptibility of Sargassum polyceratum from the deep reef slope at Carrie Bow and the reef flat at Lighthouse could result from population differences in defensive compounds or from between-reef differences in herbivorous fishes.

In general, it appears that herbivores consume a significant proportion of reef slope production and that this has resulted in strong selection for herbivore deterrents in seaweeds from this habitat. Reef flats provide predictable escapes from herbivory, and seaweeds from these habitats are characterized by very little resistance to herbivory.

ACKNOWLEDGMENTS

This study was supported by a post-doctoral fellowship from the Smithsonian Institution and by the Marine Systems Lab of the Smithsonian Institution.

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